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THE SYSTEMATIC AFFINITIES OF THE DIPTEROUS FAMILY PHORIDÆ.

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In a paper on the nomenclature of the dipterous wing published in the current number of *Psyche*, Professor Williston ('06) has again raised the much vexed question of the relationship of the Phoridæ among the families of Diptera.

During the past few years I have devoted considerable time to a study of this small and truly remarkable group of flies, but have been unable so far to reach any wholly satisfactory conclusion as to their proper systematic position. Attempts in a number of directions have each revealed some important if not insuperable obstacle, and I had let the matter rest, compelled to accept, albeit rather unwillingly, the final decision expressed by the late Baron Osten Sacken in the following words: "A real *affinity* with *Phora* does not exist anywhere."

In the nature of things such a negative opinion on a question of phylogeny can only be tentative, and it is with pleasure that I find the discussion reopened by so eminent a dipterist as Professor Williston.

Several entomologists who have given special attention to the group have attempted to reconcile its notable peculiarities of structure with types to be found elsewhere within the order of Diptera, and one has even essayed to connect them with the Aphaniptera which are almost unanimously regarded as forming a separate order.

The antennæ and the wings are the organs which offer the difficulties and I shall describe them briefly. The antenna consists apparently of a single large globular or pear-shaped joint

which bears a dorsal or terminal arista composed of three joints. When examined more closely, however, and more especially in longitudinal section, it is seen that this large segment is complex (see Fig. 1) and consists of a smaller joint almost entirely concealed within a larger outer one. These two are attached to the head by a third small and partially concealed segment. Such an arrangement is constant throughout the Phoridæ and is, so far as I know, absolutely unique among Diptera.

The nomenclature and homology of these joints has been interpreted in several ways. Wandolleck ('98) has considered the antenna to be six-jointed without attempting to homologize the segments with those of the antennæ of other Diptera. The majority of recent dipterists seem to have accepted a nomenclature which would regard the three large basal joints as homologous with the three segments of the typical brachycerous antenna, the apical one supplied with an arista of the usual kind. The third interpretation suggested in the paper before referred to by Williston ('06) is that the basal portion consists of two joints only, and that the arista so-called really represents the whole flagellum of the nemocera. Schiner also refers to the antenna as apparently two-jointed ('64, p. 335), but on page xv he says in more detail: "Fühler nahe am Mundrande eingefügt, scheinbar zwei-gliedrig, das dritte Glied rund (bei *Conicera* kegelförmig), mit nackter oder doch nur pubescenter Rücken- oder Apicalborste." It is thus evident that he takes them to be actually three-jointed, and in this view I fully concur. From the examination of large numbers of mounted specimens representing most of the described species, as well as several in microscopical section, and a number of published figures, I am fully convinced that there are always three distinct joints, the large apical one of which bears an arista.[1]

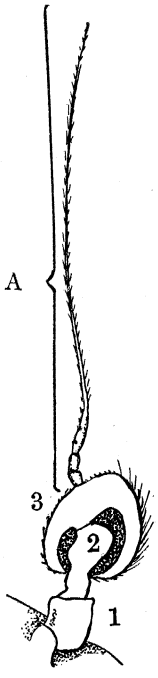

FIG. 1. Phorid Antenna. 1, 2, 3, antennal joints; *A*, arista.

[1] Whether we conceive the arista to be a modified portion of the nemocerous flagellum would in this connection be a problem apart from the relationship of the various brachycerous families among themselves.

In all species that I have examined the arista is three jointed, the two basal joints short and the other long. It thus offers no noticeable difference from the same appendage of many typical Brachycera.

Williston suggests that the Orphnephilidæ have antennæ comparable to those of the Phoridæ except for the number of aristal joints which is seven. In this case however, to judge from Schiner's description[1] the second joint is composite like the third joint of the Tabanidæ, Stratiomyidæ and allied forms. Whether the Orphnephilid antenna is in reality three-jointed I am unable to say, but the annulation of the second apical joint finds no counterpart among the Phoridæ.

Williston believes that the palpi are two-jointed, and bases a part of his argument for nemoceran affinities on this supposition. From my own observation I do not believe however, that such is the case, nor can I find any reference to this effect in the literature and published figures at hand,[2] with the exception of a single diagram by Dahl ('99, p. 75, Fig. 5) where he figures the palpi of the East Indian *Phora* (*Dorniphora*) *dorhni* with two joints. I think the accuracy of this one case can be questioned as I have identified almost certainly his species among a lot of Phoridæ from New Guinea and find the palpi single jointed as usual. Becker ('01) gives careful figures of the head with palpi in a number of genera[3] but in each case there is no indication of more than a single joint. I have studied with great care the mouthparts of several of the subapterous myrmecophilous genera, but have found no trace of a second joint. Fig. 2 is reproduced from a drawing of one of these species in which there is no trace of any articulation. The palpi of the Phoridæ are always large, and are in some instances immensely swollen (*e. g.*, *Phora palposa* Zett. and *Aphiochæta magnipalpis* Aldrich ♂) but in other respects

[1] In "Fauna Austriaca," II., 643, he says of the Orphnephilidæ: Fühler nahe am Mundrande stehend, kurz und so sich darstellend, als ob sie aus einem runden ersten, einem ovalen zweiten und einer Endborste bestünden; bei mikroscopischer Untersuchung zeigt sich, dass das zweite ovale Glied aus drei und die Endborste aus sieben walzenförmigen Gliedern besteht, deren letztes am Ende borstig ist.

[2] After this paper had gone to press, Dr. Williston called my attention to another published paper by Wesché (*Journ. R. Micr. Soc.*, 1904) in which Phorid palpi are figured as two-jointed.

[3] *Phora*, *Hypocera*, *Aphiochæta*, *Trineura* and *Metopina*.

they differ from those of the more specialized Brachycera like the Muscidea only in their more strongly developed bristles.

It is in the venation of the wings that the Phoridæ depart most strikingly from the other Diptera. This varies among the few known genera only in trivial details, so that the general type for the entire family is practically uniform. Fig. 3 shows the wing of a typical species. The veins can at once be divided into two groups, the several heavy ones which lie close together at the

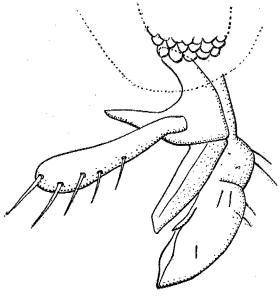

FIG. 2. *Commoptera solenopsidis* Brues, mouthparts of ♀.

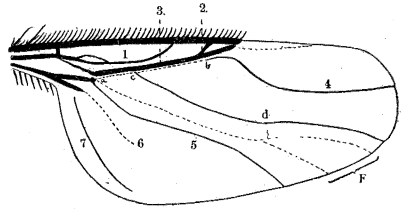

FIG. 3. Diagrammatic Phorid Wing. (After Becker.)

basal half of the wing anteriorly, and the four delicate ones which pursue an oblique course across the posterior part of the wing. This arrangement is so peculiar, that attempts to homologize the veins with those of other Diptera have proved very unsatisfactory. Several families present a somewhat similar appearance and in each case comparisons have been drawn. Williston, in the paper referred to above ('06) mentions the close similarity in venation to the Bibionid genus *Apistes*, and Becker ('01) earlier noted the resemblance to *Scatopse* another member of the Bibionidæ and to *Simulium* belonging to the Simuliidæ. It is true that there is a close superficial resemblance but no attempt has been made to homologize the veins. It is evident that *Apistes*, *Scatopse* and *Simulium* are all considerably specialized and we can indeed trace through the Bibionidæ the loss of the posterior series of veins which are quite strong in *Bibio*, weaker in *Dilophus* and still more so in *Scatopse* and *Apistes*, with a coincident strengthening of the anterior veins and their withdrawal basally. That a resemblance between this, the result of specialization within a family of closely similar forms and another otherwise widely different family

can have phylogenetic import, I am inclined to doubt. I think it can not be questioned that a complete venation is the primitive condition for the Bibionidæ, so that we cannot assume a common origin for the Bibionidæ and Phoridæ on evidence from neuration, but necessarily a *Scatopse*-like or *Apistes*-like ancestor for the Phoridæ. This is manifestly improbable as it involves after the fixation of a degenerating wing venation, vast strides in the evolution of other organs (antennæ, palpi) to give rise to Phoridæ while the parent stock remains unchanged.

Such a loss of posterior veins has occurred independently in many groups; the Stratiomyidæ and Hippoboscidæ may be mentioned among the Diptera and the Chalcididæ, Proctotrypidæ, Bethylidæ and Cynipidæ among Hymenoptera. The adaptation seems to be due to mechanical adjustment and of course not to common ancestry.

Palæontology offers but little on the history of the Bibionidæ and practically nothing on that of Phoridæ. The occurrence of *Phora* has been recognized by Berendt ('45) and Loew ('50) in Prussian amber. The bibionid genera *Protomyia*, *Bibio*, *Plecia*, and *Bibiopsis* have been found to occur together in considerable abundance in the Mayencian formation at Radoboj in Croatia (Heer, '47), while *Scatopse* is known first from the Ligurian, occurring in Prussian amber with *Phora* and also at Aix, France (Serres, '29).

In his monograph of the European Phoridæ, Becker has advanced the idea that the Phoridæ are derived from nemocerous forms allied to the Mycetophilidæ, basing his opinion principally upon a careful comparison of the wing venation of the two families made by Girschner. Girschner's view is given as follows: "Ich halte das Phora Geäder für ein modificiertes Mycetophilidengeäder, wie ich auch die Mycetophiliden für die nächsten Verwandten und Stammesangehörigen der Phoriden halte. Ich deute das Geäder in der oben skizzierten Weise (reproduced here as Fig. 3). Von *a* bis *b* ist die Discoidalader mit der Cubitalader verschmoltzen, wie dies schon angedeutet wird bei Macrocera. Bei einigen Phora-Formen kann man ziemlich deutlich — doch nicht so auffallend wie in der Zeichnung punctiert angegeben — die unter die Cubitalader hinstreichende Discoidalader wahrnehmen.

Die kleine Querader fehlt, weil die in der Strecke *ac* enthalten ist."

This comparison is very striking and were it not for the fundamental differences in metamorphosis and in other organs, might be conclusive. It is further strengthened by the fact adduced by Becker that certain of the macrochætæ covering the body are in both families provided with chitinous bristle-like projections.

On the other hand, Schiner has with almost equal facility reduced the Phorid wing to a more generalized type of brachycerous venation according to the following scheme (see Fig. 4).

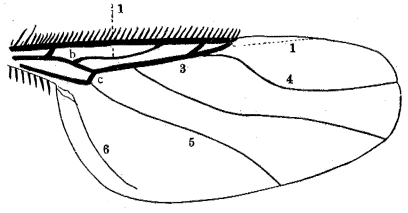

FIG. 4. Wing of *Phora* sp., as interpreted by Schiner.

The main differences between this and the arrangement by Girschner lie in the interpretation of the fourth vein involving the presence of the cross-vein and the presence of the anal vein. Schiner's designation of the indistinct thickening along the costa beyond the tip of the heavy veins as a "Fortsetzung der ersten Längsader" I cannot exactly understand, but it involves no important point.

Of the two views, that of Girschner accords more closely with the actual wing venation, and will I think be partly accepted with the exception of several points mentioned on a later page, by all who will study carefully a series of wings. That this similarity between the Mycetophilid and Phorid wing involves genetic relationship does not necessarily follow, however. As suggested on a previous page, specialization of wings often follows more or less parallel paths in diverse groups, and this seems to be especially true in those where a loss in complexity of structure is brought about by parasitism, secretive habits, or minute size. Turning to the Dipterous family Hippoboscidæ, widely removed from those previously discussed, we can see a strikingly similar condition to the one assumed by Girschner for the Phoridæ. Fig. 5 shows the wing of a species of *Olfersia*, a genus of Hippoboscidæ. The heavy veins are confined to the anterior basal region, while several oblique light veins tra-

verse the large posterior expanse. Moreover, the individual veins retain almost the same relative position in these representatives of the three families. In *Olfersia* the first, second and third longitudinal veins join the heavy costal vein, which extends for only a part of the wing length, in nearly parallel directions.

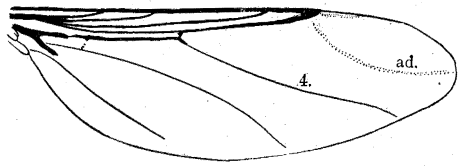

FIG. 5. *Olfersia* sp., wing. *ad*, adventitious vein; *4*, fourth vein.

The fourth is not fused with the third basally, but lies close to it so that the anterior cross-vein is extremely short. Such precisely similar developments are remarkable, and must, I think, be due to some similar tendency to degenerate in certain definite directions.[1]

Be this as it may, I think the evidence is sufficient to show that direct descent from Mycetophilid-like forms is not a logical necessity in tracing a genealogy which will account for the similar wing venation of the Phoridæ.

Several other attempts to discover relationships that have been less elaborately worked out are enumerated in the papers by Osten Sacken ('02) and Coquillett ('01). There is no agreement as to whether they belong properly to the Orthorrapha or Cyclorrapha. Osten Sacken (*l. c.*) refers them to his orthorraphous superfamily Energopoda which contains the Asilidæ, Empididæ, Lonchopteridæ and Phoridæ, while Coquillett has proposed the orthorraphous superfamily Phoroidea to contain the Lonchopteridæ and Phoridæ. Mik thought he saw Borborid affinities, as he says ('98, p. 205): "Aenliche Mundtheilen . . . findet man bei den Borboriden, mit welchen die Phoriden wahrscheinlich nahe verwandt sind."

The concensus of recent opinion associates the Lonchopteridæ and Phoridæ together with apparent good reason. The head, form of front with its macrochætæ, proboscis, palpi, antennæ with their arista, bristly thorax and legs, large, freely articulated ante-

[1] Such an idea savors of orthogenetic principles, although in an unusual sense, offering an interesting field for speculation, and for comparative studies as well.

rior coxæ, and the general habitus and actions when alive are very similar in both families. On the other hand the wing venation is different, but taken in connection with the facts already presented showing similar degeneration in so many families, this is not so great an objection as it would be otherwise.

Aside from Mik, dipterists do not appear to have detected many affinities with muscid forms. I am nevertheless inclined to agree with him that the Phoridæ show a relationship with the Borboridæ. This may quite probably also have been Schiner's idea when he placed the Phoridæ between the Bibionidæ and Borboridæ, rather than to show relationship to the former family as Williston suggests ('06). The various points of resemblance are: first, their similar appearance and actions when alive, they are the only family whose motions when running or flying could be confused with those of the Phoridæ; the modification of the incrassated hind metatarsi, the same segment being modified by rows of scaly bristles in every member of the Phoridæ, even the wingless forms and Termitoxenia; the tendency shown in the Borboridæ to lose certain of the apical and posterior parts of the veins in the wing and the tendency also to develop wingless forms like the Phoridæ. However, the legs and head of the Borboridæ are not bristly to any extent. Other differences are mainly the ones that appear equally in comparison with any family.

It is therefore in my opinion probable that the Lonchopteridæ and Phoridæ may together find a more suitable place in the Cyclorrapha rather than at the end of the Orthorrapha where placed by Coquillett. This is what Williston has done with them in the second edition of his manual ('96) where they are placed between the Platypezidæ and the Muscidea. At least there seem fewer objections to this course than to any other.

Regarding the nomenclature of the wing veins of the Phoridæ there has been considerable difference of opinion as mentioned on a previous page, and I would like to correct what I think is an error in the identification of the fourth and fifth veins. The first oblique light vein has been considered by various writers (Schiner, '62, Comstock, '94, Becker, '01, Brues, '04) as the fourth longitudinal vein, but I now believe that the second light

vein represents the fourth and that what has been called the fourth is an adventitious vein. The process of coalescence in the Hippoboscidæ has suggested this.[1] Here (see Fig. 6) the first light vein arises at the cross-vein which is near the middle of the third vein. This vein is undoubtedly the fourth on account of its association with the posterior end of the cross-vein yet it occupies exactly the same place as the second light vein in the Phoridæ. This is a far more probable sort of coalescence by shortening of the cross-vein than an approximation of veins throughout their entire length which would be necessary to bring the fourth vein near the tip of the the third where the adventitious vein originates. Other points in favor of an adventitious origin are the appearance in some cases of a nebulous thickening in the same space in the Hippoboscid wing and the great variability of this vein in the Phoridæ. It also removes the difficulty which Coquillett saw in recognizing three posterior veins in the Phoridæ which he thought would exclude them from membership in the Cyclorrapha. I think also that the slight thickening near the costa beyond the tip of the third vein is also an adventitious vein if it can properly be designated as a vein.[2]

I agree with Girschner and Becker that the sixth (anal) vein is lost, or obsolete, and that the last vein (fourth light vein) represents the seventh or axillary. There can be no doubt that the short anterior branch at the tip of the third vein represents the second which is fused with it to this point. In the more specialized genera (*e. g.*, Hypocera, Puliciphora) the fusion is complete to the tip..

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[1] There are many other developments among the Phoridæ which parallel those of the pupiparous Diptera such as the Hippoboscidæ. Briefly summarized they are (1) The degeneration and sometimes ultimate disappearance of the wings. (2) The production in the apterous or subapterous forms of very large eggs which distend the abdomen greatly and are even thought in some cases (cf. Wasmann,'02) to develop to the larval or pupal stage before being laid. (3) The similarity in wing venation already mentioned. (4) The degeneration of the eyes (cf. Streblidæ, Brues, 04[a], Fig. 1).

These resemblances are undoubtedly the result of parallel development, but as Professor Williston has suggested to me in a recent letter, they tend to weaken the value of the group Pupipara.

[2] Schiner refers to it as a part of the first vein.

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